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NEST DEFENSE BY MALE AND FEMALE SPANISH IMPERIAL EAGLES

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ABSTRACT.—Sexual differences in nest defense behavior in response to human intruders were studied in the Spanish Imperial Eagle (*Aquila adalberti*). Females defended the nest more than males, and their defense increased as the breeding cycle progressed. The defensive behavior of the female was independent of male presence.

Defensa del nido por progenitores de Aguila Imperial Ibérica

EXTRACTO.—Se estudian las diferencias entre sexos en el comportamiento de defensa del nido, en respuesta a la presencia humana, en el Aguila Imperial Ibérica (*Aquila adalberti*). Las hembras defienden el nido más que los machos, y su comportamiento defensivo aumenta al avanzar el ciclo reproductivo. El comportamiento defensivo de la hembra es independiente de la presencia del macho.

Diurnal raptors exhibit three strategies of nest defense: principally by the female, by both sexes, or principally by the male (Mueller and Meyer 1985, Andersson and Wiklund 1987). There are also differences in the division of other roles associated with reproduction, such as incubation, provisioning of food, feeding the young and surveillance (Cramp and Simmons 1980, Mueller and Meyer 1985). In the Spanish Imperial Eagle (*Aquila adalberti*), incubation and care of chicks in the nest are principally carried out by the female (Cramp and Simmons 1980), but it is unknown whether or not there are sexual differences in offspring protection. Several authors have suggested that the general trend towards reversed sexual dimorphism in the Falconiformes may be at least partly an evolutionary response to sexual differences in nest defense (Snyder and Willey 1976, Andersson and Norberg 1981, Andersson and Wiklund 1987). Information on the division of nest defense between the sexes is scarce in raptors (Mueller and Meyer 1985), however.

Recently Andersson and Wiklund (1987) studied nest defense in the Rough-legged Buzzard (*Buteo lagopus*) and found that the smaller males undertake

most of the defense. Although contrary to the prediction, this result does not refute the hypothesis. The evaluation of such an evolutionary hypothesis necessitates a comparative analysis seeking repeated patterns throughout the order (Pages and Harvey 1988). In this study, I examine the contribution of male and female Spanish Imperial Eagles to nest defense against human intruders.

METHODS

The study was undertaken in Doñana National Park in southwest Spain from 1974–1988. Observations were made during 201 visits to 51 nests of 15 different pairs. A visit involved one person climbing to the nest to record breeding stage and examine eggs or young. During the visit I recorded the sex, and distance from the nest and attack behavior of the adults. Even though the sexual dimorphism is slight (mean weight was 2613 g [N = 16] for males, and 3467 g [N = 21] for females, Ferrer unpubl. data), it was possible to assign sex to adults with confidence approximately 50% of the time, using individual differences in moult and observations of the two members of the pair together. Nest defense was classified into three categories based on the distance the adults kept from the person investigating the nest: 1) >50 m when the adult remained more than this distance from the nest while the chicks were handled or the eggs examined, 2) <50 m when

Table 1. Observations of nest defense by Spanish Imperial Eagles according to distance classes and sex (0 m corresponds to direct attack).

DISTANCE	MALE		FEMALE	
	INCUBATION	NESTLING STAGE	INCUBATION	NESTLING STAGE
>50 m	10	8	15	9
<50 m	2	2	9	17
0 m	0	1	2	10
Total	12	11	26	36

the adult remained closer than this distance and, 3) 0 m when the adult attacked the observer. Statistical analyses for evaluating the significance of nest defense variations were performed using N X M exact test (Wells and King 1980).

RESULTS

In 85 observations the sex of attending adults was recorded. The female was always present, while the male was present on only 23 occasions (27%). The single versus paired ratio during visits in which the sex of the adults could not be identified ($N = 116$) was 41.3%. Females remained closer and made more attacks than males (Table 1; $\chi^2 = 10.65$, $P = 0.005$). During incubation, females were not significantly more aggressive than males ($\chi^2 = 2.66$, $P = 0.269$). However, during the nestling stage the female was more aggressive than the male ($\chi^2 = 8.32$, $P = 0.015$).

Males did not differ significantly in defense activity between incubation and nestling stages ($\chi^2 = 1.18$, $P = 0.784$). In contrast, females increased defense significantly in the later stage of the nesting cycle ($\chi^2 = 7.89$, $P = 0.019$). The responses of females did not differ in the presence of males (Table 2, incubation $\chi^2 = 0.35$, $P = 0.834$, nestling $\chi^2 = 0.04$, $P = 0.978$).

DISCUSSION

In the Spanish Imperial Eagle, incubation and the care of chicks in the nest are principally carried out by the female (Cramp and Simmons 1980). This was evident from our data, as we never observed the male alone at a nest, and we frequently observed females alone. During incubation, males provide food, while females are spending more time at the nest. Females defended more than males. This is in agreement with the hypothesis that the maintenance of reversed sexual dimorphism favors larger females which can better defend the nest against predators

Table 2. Observations of female Spanish Imperial Eagles defending their nests in relation to presence or absence of the male (0 m corresponds to direct attack).

DISTANCE	INCUBATION		NESTLING STAGE	
	MALE PRESENT	MALE ABSENT	MALE PRESENT	MALE ABSENT
	>50 m	8	8	3
<50 m	3	5	5	12
0 m	1	1	3	7
Total	12	14	11	25

(Snyder and Willey 1976, Andersson and Norberg 1981).

Recently, some authors (Wiklund and Stigh 1983, Andersson and Wiklund 1987) have presented an alternative hypothesis for the maintenance of reversed sexual dimorphism in Falconiformes. Although still arguing that nest defense is an important selection pressure, they suggest that the selection would not be to increase female size, but rather to decrease male size. This would enhance flying agility and reduce the risk of defending the nest against predators of larger size, including human intruders (Andersson and Wiklund 1987). This hypothesis is not supported by our data because the smaller males did not defend the nest vigorously. Additionally, Pleasants and Pleasants (1988) have suggested that sexual dimorphism evolved through an increase in female size and not a decrease in male size, at least in diurnal raptors.

My data show a rise in female nest defense behavior as the breeding cycle progresses, a decrease in distances from the observers and an increase in the frequency of attacks. In contrast, males did not increase their defensive efforts along the breeding cycle. Similar results have been found in Merlins (*Falco columbarius*) by Wiklund (1990). He suggested that male investment in nest defense influenced mate selection by females. Consequently, later in the breeding cycle a greater investment is not necessary for males. The increase in female defensive behavior could be more related with the age of the chicks and accumulated investment (Andersson et al. 1980). Nevertheless, Ferrer et al. (in press), reported a rise in nest defense over the years in this eagle population, suggesting that this increase can be attributed to experienced adults whose defense behav-

ior has been positively reinforced upon not losing their offspring after a hypothetical predatory attack (Knight and Temple 1986). The fact that females spend more time at the nest and, consequently, they probably have more previous experiences with human intruders than males, could explain, at least in part, the increase of aggressive behavior detected in this sex.

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